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Gut contents of some lumbricid earthworms

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1. Introduction

A single fertile pasture soil in Britain may support eight or more species of lumbricid earthworm (GUILD 1951 and SATCHELL 1955). In view of the variety of feeding habits exhibited by the Lumbricidae (GATES 1961, DUNGER 1963, RHEE 1963, ZICSI 1966, BOUCHÉ 1972, BOUCHÉ and KRETZSCHMAR 1974, and PIEARCE 1972a) it is of interest to determine the extent to which such co-existing species differ in diet. This paper presents a quantitative assessment of the nature of the material consumed by selected species inhabiting a permanent pasture soil in North Wales.

2. Materials and methods

Details of the location, soil characteristics, flora and lumbricid fauna of the permanent pasture site at Aber, near Bangor, have been given previously (PIEARCE 1972b). This site was chosen for special study because its brown earth soil supported a variety of lumbricid species in abundance. The investigation was confined to adult specimens only, on the assumption that these would reflect the clearest differences in diet, and to six of the twelve species present, *Allolobophora caliginosa* (SAVIGNY), *A. chlorotica* (SAVIGNY) [green form], *A. longa* UDE, *Dendrobaena mammalis* (SAVIGNY), *Lumbricus castaneus* (SAVIGNY) and *L. rubellus* HOFFMEISTER, all of which were easily obtained in large numbers.

Thirty specimens of each species were collected in the autumn of 1970, at which time of year many species reach peak abundance and activity (EVANS and GUILD 1947, GERARD 1963 and SATCHELL 1967). The animals were rapidly extracted from the soil by digging and hand-sorting, dropped immediately into liquid air and brought back to the laboratory where the crop and gizzard contents were dissected out and inspected microscopically. Three major dietary components were distinguished: recognisable mineral particles (''mineral matter''), recognisable organic fragments (''organic fragments'') and a complex of organic matter in an advanced state of decay, without visible structure, with fine organic particles (''amorphous matter''). The relative proportions of these, and of various minor components, was assessed as ''abundant'', ''present'' or ''absent'', and a record made of the occurrence of different types of recognisable plant material. The maximum length and width of organic and mineral particles in each sample was measured.

When lumbricids are frozen in liquid air very soon after removal from soil, subsequent thawing and dissection reveals swellings along the oesophagus containing soil, each of which is generally quite distinct from its neighbours. These aggregates of ingested material have the appearance of boli travelling from the pharynx to the crop. Their number and size were recorded for each species.

A further twenty-four specimens of *D. mammalis* and thirty of the other species, collected by digging and hand-sorting, were transported quickly to the laboratory, washed, rough-dried on moist filter paper, and weighed, before being placed in separate Petri dishes and kept at 10 °C in the dark for three days. At the end of this period the faeces produced were dried to constant weight at 100 °C and their organic content determined as weight loss on ignition at 450 °C.

The relative abundance of "organic fragments" and "amorphous matter" in the crop and gizzard contents were compared between species by calculation of χ^2, taking $P < 0.05$ for significance. Since the quantity of material in the crop and gizzard increases with the size of the animal, measurement of the proportion of samples in which a particular component is present will give an estimate of relative abundance biased towards the larger species. This difficulty was overcome by basing interspecific comparisons on the numbers of items in "abundant" and combined "present" and "absent" categories. Mean particle and bolus size, fresh body weight, faecal dry weight and weight loss on ignition were compared using "Student's" "t" test ($P < 0.05$ for significance).

3. Results

Mineral particles were abundant in the ingesta of all species (Table 1). Significant differences were found in the proportions of "organic fragments" to "amorphous matter" consumed, *L. castaneus* and *L. rubellus* taking more "organic fragments" than any of the other species, *A. caliginosa* and *A. chlorotica* less. The majority of recognisable plant remains were fragments of Gramineae leaves and fibrous material (Table 2), although roots, seeds and other plant parts were occasionally found. Algae were the most abundant visible micro-organisms (Table 3). Fungi and testacean Protozoa were frequently present, together with pieces of arthropod cuticle. More rarely, nematodes and enchytraeid setae were recorded.

Table 1. Major components of crop and gizzard contents

Species	Component					
	"Organic fragments"		"Amorphous matter"		"Mineral matter"	
	++	+	++	+	++	+
A. caliginosa	9	10	25	5	25	4
A. chlorotica	6	13	20	10	28	0
A. longa	20	6	17	12	17	13
D. mammalis	13	12	9	13	25	4
L. castaneus	21	9	6	15	18	12
L. rubellus	26	4	15	10	20	9

Note. — Relative abundance expressed as number of samples out of thirty in which each item was abundant (++) or present but not abundant (+).

Table 2. Recognisable plant remains in crop and gizzard contents

Species	Component						
	Fibres	Grass leaves	Setae	Dicotyledonous leaves	Roots	Nodes	Seeds
A. caliginosa	21	9	1	1	1	0	0
A. chlorotica	14	9	0	0	1	0	0
A. longa	22	16	1	1	2	1	1
D. mammalis	13	12	0	1	0	0	0
L. castaneus	27	18	2	1	0	2	0
L. rubellus	25	22	0	2	1	0	1

Note. — Occurrence in thirty samples.

Table 3. Minor components of crop and gizzard contents

Species	Component							
	Algae		Fungi		Testaceans		Arthropod cuticle	
	++	+	++	+	++	+	++	+
A. caliginosa	18	12	0	26	0	10	1	12
A. chlorotica	22	8	0	11	1	6	0	11
A. longa	14	16	3	25	1	16	0	11
D. mammalis	17	13	3	19	7	10	5	13
L. castaneus	21	9	3	21	4	14	1	19
L. rubellus	21	9	2	23	1	18	1	16

Note. — Relative abundance expressed as number of samples out of thirty in which each item was abundant (++), or present but not abundant (+).

The ratio of dry faecal weight: fresh body weight was significantly lower for *A. chlorotica* and *L. castaneus* than for any of the other species; faecal weight loss on ignition was significantly higher for *L. castaneus* than for any other species, and significantly lower for *D. mammalis* (Table 4). The crop and gizzard contents of the two largest lumbricids, *A. longa* and *L. rubellus*, contained significantly larger mineral particles than the others (Table 5) and significantly larger organic fragments than all except *L. castaneus*. Mean bolus size (Table 6) was also significantly greater for the two largest species, but bolus number showed a different pattern, significantly higher in *A. caliginosa* and *A. longa* than in the *Lumbricus* species or *D. mammalis*.

4. Discussion

Examination of the nature of lumbricid gut contents and faeces provides only an indirect indication of nutritional requirements since soil is consumed for purposes other than feeding (for example, in the creation and extension of burrow systems; BARLEY 1959) and the majority of plant detritus ingested passes through the alimentary canal without extensive degradation. Nevertheless, measurement of the relative proportions of different materials consumed will indicate broad similarities and differences in diet between species.

Table 4. Faecal output and percentage weight loss on ignition

Species	Fresh body wt. (mg) Mean ± S.E.	Faecal dry wt. (% fresh body wt.) Mean ± S.E.	Faecal L.I. (%) Mean ± S.E.
A. caliginosa	541 ± 6	*5.53 ± 0.32*	*14.6 ± 0.51*
A. chlorotica	409 ± 20	*3.58 ± 0.40*	*15.9 ± 1.19*
A. longa	2,761 ± 121	*4.85 ± 0.40*	*19.9 ± 1.31*
D. mammalis	192 ± 14	*5.15 ± 0.44*	*9.7 ± 0.49*
L. castaneus	283 ± 13	*3.31 ± 0.24*	*26.2 ± 1.70*
L. rubellus	829 ± 45	*4.88 ± 0.44*	*17.2 ± 1.42*

Note. — Twenty-four specimens of *Dendrobaena mammalis*, thirty of other species.

Table 5. Maximum particle sizes of mineral and identifiable organic components of crop and gizzard contents

Species	Mineral particles		Identifiable organic fragments	
	Length (mm) Mean ± S.E.	Width (mm) Mean ± S.E.	Length (mm) Mean ± S.E.	Width (mm) Mean ± S.E.
A. caliginosa	0.76 ± 0.05	0.55 ± 0.04	3.00 ± 0.42	0.37 ± 0.06
A. chlorotica	0.58 ± 0.05	0.41 ± 0.03	2.14 ± 0.26	0.37 ± 0.05
A. longa	1.01 ± 0.09	0.75 ± 0.06	9.10 ± 2.39	0.70 ± 0.09
D. mammalis	0.62 ± 0.05	0.45 ± 0.03	1.83 ± 0.19	0.40 ± 0.05
L. castaneus	0.68 ± 0.06	0.46 ± 0.03	5.59 ± 0.85	0.62 ± 0.07
L. rubellus	1.07 ± 0.09	0.79 ± 0.06	7.22 ± 1.11	0.76 ± 0.06

Note. — Thirty samples per species.

Table 6. Number and dimensions of food boli and occurrence of ingesta in pharynx

Species	No. of boli Mean ± S.E.	Bolus length (mm) Mean ± S.E.	Bolus width (mm) Mean ± S.E.	No. specimens with ingesta in pharynx
A. caliginosa	2.53 ± 0.23	0.88 ± 0.06	0.83 ± 0.04	15
A. chlorotica	1.50 ± 0.27	0.94 ± 0.09	0.82 ± 0.05	11
A. longa	1.80 ± 0.25	1.68 ± 0.10	1.45 ± 0.07	12
D. mammalis	0.87 ± 0.17	1.34 ± 0.15	0.59 ± 0.05	5
L. castaneus	1.10 ± 0.16	1.46 ± 0.18	0.92 ± 0.09	8
L. rubellus	1.00 ± 0.21	1.74 ± 0.17	1.25 ± 0.12	6

Note. — Thirty samples per species.

From the results of the microscopic examination of crop and gizzard contents, *L. castaneus* and *L. rubellus* may be described as consumers of material rich in relatively undecomposed plant remains, and *A. caliginosa* and *A chlorotica* as feeders on well-decomposed detritus, characterisations supported by the results of other studies (Dunger 1963, Rhee 1963, Zicsi 1966 and Piearce 1972a). *Allolobophora longa* and *D. mammalis* appear to be intermediate in diet. The former species has been reported as taking leaves (Støp-Bowitz 1969), and grass leaf fragments were a major part of the material ingested at the Aber site. *Allolobophora longa* readily ingests seeds of *Poa pratensis* L. and *Phleum pratense* L. in the laboratory (Huffer pers. comm.); the present study has shown that seed consumption may commonly occur in this species, and in the litter-feeding *L. rubellus*, in the field. The occurrence of root fragments in the ingesta of *Allolobophora* spp. and *L. rubellus* lends support to the view that some species may be root browsers (Waters 1955 and Gerard 1963).

Atlavinytė and Počienė (1973) have shown that algae are digested by lumbricids and there is evidence that fungi (Parle 1963) and testaceans (Miles 1963) are utilised as food by some species. On the basis of their relative abundance in the present study, algae, and to a lesser extent fungi, are possibly of some importance in the nutrition of all six species, testaceans in the nutrition of *D. mammalis*.

The maximum size of particles in the crop and gizzard contents is a crude measure of the limit of size of particle ingested. For mineral material it followed the body size sequence, but for organic matter there was one marked exception to the general trend, *L. castaneus*, the second smallest species, took larger fragments than the moderate-sized *A. caliginosa* and *A. chlorotica*, a reflection of the litter-feeding habit of this species. The low dry faecal weight: fresh body weight ratio of *L. castaneus* may be related to the low weight per unit volume of the relatively undecomposed organic material that forms a large part of its diet: the significantly higher faecal weight loss on ignition of this species compared with the other five is a further reflection of its litter-feeding behaviour.

Aggregations of ingested material in oesophageal swellings remained discrete, more or less rounded structures, in which long fibrous fragments were frequently tightly curled, even when the specimens had thawed completely and their muscles relaxed. They were abundant in large (slow to freeze) and small (rapidly freezing) individuals. The evidence therefore suggests that the structures were true boli and not artefacts resulting from the rapid contraction of the oesophageal wall muscles on freezing. Formation of such boli will be facilitated by peristaltic contractions of the pharyngeal and oesophageal walls, and perhaps by flexures of the oesophageal wall during locomotion, as described by Arthur (1965).

Values for bolus size reported here correspond closely to those for "bite" size given by Dunger (1963) for *A. caliginosa* and *L. rubellus*. The greater number of boli in the oesophagus of *A. caliginosa* and *A. longa* than in the species of *Lumbricus* and *D. mammalis* may indicate **(a)** more regular feeding and/or **(b)** lower throughput of material in the oesophagus. Previous work has shown that ingested material passes through the gut of *A. caliginosa* more quickly than through that of *L. rubellus* (Piearce 1972a). The proportion of specimens with material present in the pharynx was greater for *A. caliginosa* than for *L. rubellus* in the present study, consistent with the view that this amorphous humus feeder consumes soil more regularly, and processes the material it consumes more rapidly, than does the litter feeder.

In conclusion, the six species studied fall into five separate dietary groups between which significant differences have been demonstrated. There is considerable interspecific overlap in the nature of the material consumed, this being greatest for *A. caliginosa* and *A. chlorotica*.

5. Summary · Zusammenfassung

There is considerable overlap in the diets of adults of six species of Lumbricidae sympatric in permanent pasture soil at Aber, North Wales, but five ecological groups can be distinguished on the basis of the nature, size and rate of consumption of organic and mineral matter.

Darminhalte einiger Regenwurmarten

Es gibt beträchtliche Überlappungen bei der Nahrungsaufnahme adulter Exemplare von sechs sympatrischen Lubricidenarten im Boden einer Dauerwiese bei Aber, Nordwales. Auf Grund von Art, Größe und Konsumptionsrate der organischen und mineralischen Substanz können ökologisch fünf Gruppen unterschieden werden.

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